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RESPIRATORY ADAPTATIONS OF THE ESTUARINE MUD SHRIMP, *CALLIANASSA JAMAICENSE* (SCHMITT, 1935) (CRUSTACEA, DECAPODA, THALASSINIDEA) [1]

DARRYL L. FELDER

Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504

Thalassinid mud shrimps commonly burrow in hypoxic marine sediments, and their success in these habitats seems, at least in part, predicated upon metabolic adaptations. Recent studies of thalassinids from the Pacific coast of North America have identified a number of behavioral and physiological respiratory adaptations to the hypoxic habitats of intertidal species (Farley and Case, 1968; Thompson and Pritchard, 1969; Roxby, Miller, Blair, and Van Holde, 1974; Miller and Van Holde, 1974; Miller, Pritchard, and Rutledge, 1976; Torres, Gluck, and Childress, 1977; Hawkins, 1971, unpublished M.S. thesis, Oregon State University). A rich thalassinid fauna occurs in intertidal and sublittoral habitats along coasts of the western Atlantic, but metabolic regulation among these species has been investigated only in *Upogebia affinis* by Mangum and van Winkle (1973).

The present study concerns *Callianassa jamaicense* (Schmitt) (*Callichirus jamaicense* according to the generic scheme of de Saint Laurent, 1973), a common inhabitant of estuarine mud flats in the northern Gulf of Mexico (Felder, 1978) and other areas of the western Atlantic (Rodrigues, 1971). On the Louisiana coast, dense populations of *C. jamaicense* are found in muddy substrates where low-salinity interstitial water is markedly hypoxic. Tidal exposure of these substrates frequently subjects such populations to extended periods of anoxia. Studies were undertaken to identify respiratory adaptations of *C. jamaicense* to such hypoxic habitats. Specifically, this paper reports (i) survival under aquactic and aerial anoxia, (ii) aerial respiration, (iii) effects of oxygen tension on metabolic rate, and (iv) post-anoxia metabolic rates.

Materials and Methods

Animals were collected from a tidally influenced pond on Grand Terre Island, Louisiana. Methods of collecting, transporting, maintaining and salinity-acclimating animals were the same as previously described (Felder, 1978). Animals were acclimated to a salinity of 20‰ in dark, 25° C incubators; all were maintained at this salinity for nine days before experiments were initiated. Animals were not fed, and aeration was provided during all phases of salinity-acclimation. Only intermolt, uninjured adult males were used in respiration studies. Wet weights were determined by thoroughly blotting animals with tissue and then weighing to the nearest milligram. All sea water used in experimental studies was carefully maintained at a salinity of 20 ± 0.3‰ and temperature of 25 ± 0.2° C.

Anoxic sea water was prepared by gassing sea water with nitrogen. In one

[1] In part adapted from a doctoral dissertation submitted to the Department of Zoology and Physiology, Louisiana State University, Baton Rouge.

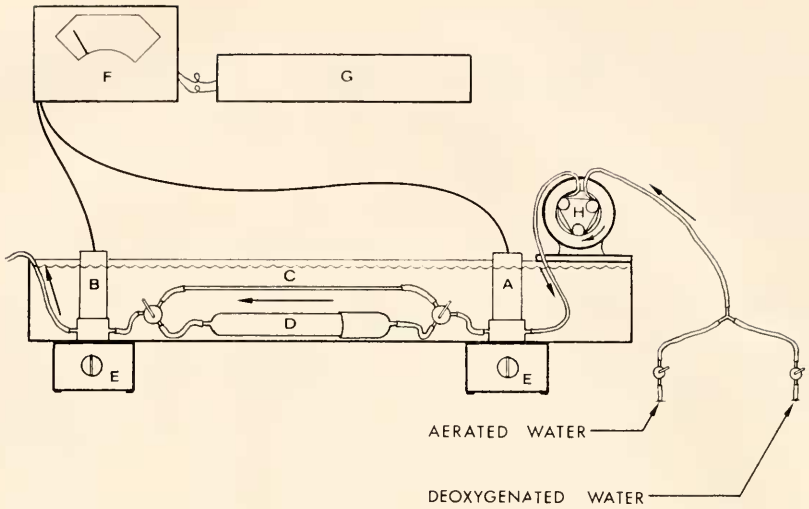

FIGURE 1. Diagrammatic cut-away view of water bath showing components of flow-through respirometer: A, influent oxygen electrode; B, effluent oxygen electrode; C, bypass shunt; D, respiration chamber; E, magnetic stirrers; F, differential oxygen meter; G, integrating chart recorder; H, peristaltic pump. A small bubble trap (not shown) was installed between components H and A.

experiment anoxic sea water was siphoned into BOD (300-ml biochemical oxygen demand) bottles containing one animal each, and bottles were sealed until death occurred. Other animals in individual, perforated vials were placed as a group into 5 liters of anoxic sea water which was replaced daily; whenever the 5-liter jar was opened for removal of dead animals, it was regassed with nitrogen. Control animals were maintained in continuously aerated sea water. Tolerance of aerial anoxia was determined by supporting animals on the rack of a desiccator over water and continuously gassing the water with nitrogen. Control animals in an aerial environment were likewise maintained, but underlying water was gassed with air.

Aerial $\dot{V}_{O_2}$ was measured in a Gilson respirometer with 130-ml respirometry flasks and equivalent ballast. Filter paper wicks and 30% KOH were added to each flask side-arm to absorb CO_2. Each flask contained one animal and one milliliter of sea water to maintain water saturation of air. One hour was allowed for equilibration; thereafter oxygen consumption was read at 30-min intervals.

Oxygen consumption at decreasing oxygen tensions was measured by placing the animal into a 13.5-mm ID (inner diameter) plastic tube with openings at both ends. The tube was wedged vertically against the wall of a BOD bottle, and a small stirring bar was placed at the center of the bottle. An oxygen electrode was fitted snugly into the bottle opening, and depletion of oxygen was recorded with a Beckman oxygen analyzer. The analyzer was calibrated in air-saturated sea water and checked by Winkler titration (Strickland and Parsons, 1972) before each run. Temperature was maintained by a water bath supported over the magnetic stirrer. The stirring rate was set at the lowest speed, which produced maximum deflection of the oxygen meter. The displacement volume of the animal, tube, and stirring bar

was subtracted from the bottle volume. Pleopod ventilatory strokes were counted during 5-min intervals and expressed as mean number/min. To minimize effects of handling, each animal was transferred to a plastic tube and placed (anterior end up) into a BOD bottle 30 min before it was sealed; as an additional precaution, the first 30 min of recorded oxygen depletion were discarded.

A flow-through respirometer was assembled from a dual-probe International Biophysics differential oxygen analyzer, a Houston Instrument integrating chart recorder, a peristaltic pump, two magnetic stirrers, a constant temperature water bath, and a 16-mm ID glass respiration chamber (Fig. 1). Flow rate was maintained at *ca.* 10 ml/min and was precisely determined by measuring the volume of effluent; injection of a dye at this flow rate indicated thorough mixing of water as it passed through the respiration chamber. Each animal was placed into the chamber with its anterior toward the influent opening; aerated water was provided for 1 hr before oxygen consumption was read. Prior to each run, the oxygen analyzer was calibrated by Winkler titration and the differential between the electrodes was set to zero. Altered oxygen tensions were achieved by controlled mixing of fully aerated and nitrogen-saturated water. Whenever oxygen content of influent water was altered, 20 min were allowed for the flow-through system to flush before oxygen consumption was read. Anoxic conditions were provided by pumping deoxygenated water into the respiration chamber and then closing valves at either end (Fig. 1). The flow-through respiration chamber was lined with fine-mesh plastic gauze to provide traction for thoracic legs during pleopod beating. Pleopod strokes were counted as previously described.

Field measurements of oxygen in exposed and submerged burrows were made during an afternoon low tide in July 1972. Oxygen concentration of water over-

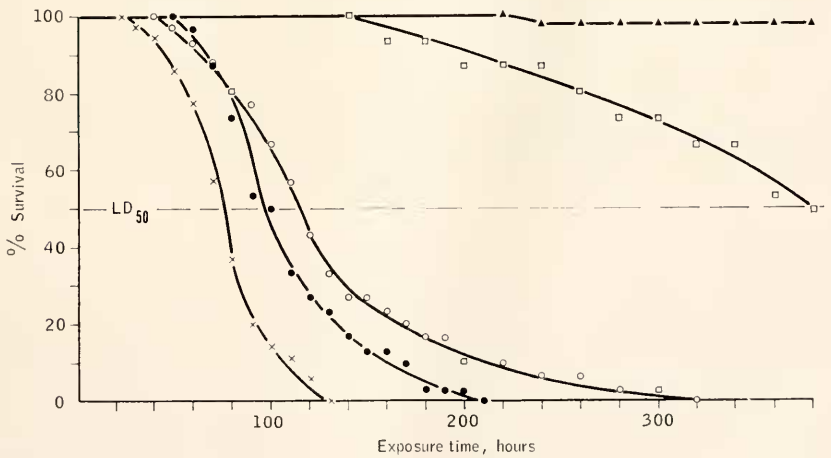

FIGURE 2. Survival among specimens of *Callianassa jamaicense* under aerial and aquatic anoxia compared to survival of controls under normoxia. Experimental conditions include anoxic water with accumulation of metabolic wastes (crosses) ($N = 35$), anoxic water changed daily (solid circles) ($N = 30$), aerial anoxia (open circles) ($N = 30$), aerial normoxia (squares) ($N = 15$), and aquatic normoxia (triangles) ($N = 50$); N is the number of animals initially exposed to each condition. Temperature was maintained at $25 \pm 0.2°$ C; salinity was $20 \pm 0.3‰$.

lying *C. jamaicense* burrows was measured *in situ* with an air-calibrated Yellow Springs Instrument oxygen meter. Water from burrows of *C. jamaicense* was sampled and analyzed as described by Thompson and Pritchard (1969).

Results

Survival under anoxia

Survival of specimens of *C. jamaicense* under aquatic and aerial anoxia is plotted in Figure 2. The LD_{50} (mean lethal dose) was lowest, *ca.* 3.2 days, when anoxic water was not changed and metabolic wastes accumulated for the duration of survival. Under such conditions, with individual animals sealed into 300-ml BOD bottles of anoxic water, ambient pH dropped from an intial level of 8.7 ± 0.3 to 6.9 ± 0.5 at the time of death. When anoxic water was replaced daily, the LD_{50} increased to *ca.* 4 days. The LD_{50} for animals held in aerial anoxia, *ca.* 5 days, exceeded that for animals subjected to aquatic anoxia. Among those animals subjected to aerial anoxia or daily changes of anoxic water, a few survived more than two times the exposures producing LD_{50}'s.

Under normoxic conditions, losses of control animals in a water-saturated environment approached the LD_{50} on the 16th day of exposure. Mortalities among control animals in normoxic water did not exceed 2% within the same 16-day time period.

Aerial oxygen consumption

After 60 min of equilibration in a 25° C Gilson respirometer, oxygen consumption ($\dot{V}_{O_2}$) in water-saturated air was read at 30-min intervals over an additional 2-hr period. Wet weights of the 25 animals used in the aerial respiration experiments ranged from 3.51 to 5.25 g. Mean $\dot{V}_{O_2}$ rates and standard errors over the four successive 30-min time periods were 18.9 ± 1.53, 16.2 ± 1.29, 19.0 ± 1.39, and 18.9 ± 1.12 μl/(g wet wt·hr), respectively. Activity in the respirometer flasks was not quantitatively monitored, but animals were for the most part quiescent during the $\dot{V}_{O_2}$ determinations.

Effects of low oxygen tension on aquatic oxygen consumption

As oxygen was depleted from sealed BOD bottles, specimens of *C. jamaicense* regulated $\dot{V}_{O_2}$ until oxygen tension (P_{O_2}) decreased to *ca.* 20 mmHg (Fig. 3). The critical oxygen tension (P_c) ranged from 10 to 25 mmHg among the 10 animals studied. The slightly higher $\dot{V}_{O_2}$ at 120 mmHg is of questionable significance as it may relate to disturbance of animals when placing them into the BOD bottles at the beginning of the experiment. Mean pleopod ventilatory rates ranged from 20 to 33 strokes/min at oxygen tensions above the P_c. As P_{O_2} fell from 20 to 10 mmHg, pleopod activity increased to near 60 strokes/min; concurrent increases in $\dot{V}_{O_2}$ occurred in some animals and accounted for the large range of $\dot{V}_{O_2}$ at oxygen tensions between 12 and 15 mmHg (Fig. 3). Pleopod activity decreased as P_{O_2} dropped below 9 mmHg and was again near 39 strokes/

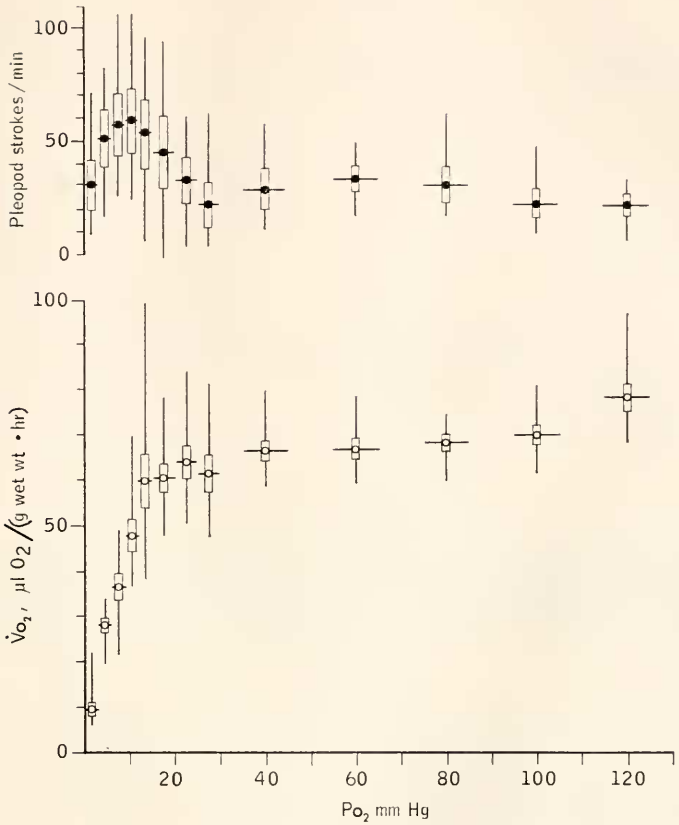

FIGURE 3. Mean oxygen consumption (open circles) and mean ventilatory rate (solid circles) among specimens of *Callianassa jamaicense* as oxygen is depleted from a sealed bottle. Each open circle is mean value for 10 animals and each solid circle is mean value for eight animals. Vertical lines indicate ranges; rectangles indicate standard errors; horizontal lines indicate span of oxygen tension over which means are taken. Wet weights range from 1.45 to 3.82 g. Temperature was maintained at 25 ± 0.2° C; salinity was 20 ± 0.3‰.

min at 0 mmHg. Animals held at complete anoxia continued to decrease pleopod activity and, after 2 to 4 hr, stopped ventilating unless disturbed.

When P_{O_2} was abruptly decreased from normoxia (150 mmHg) to hypoxia (37 mmHg) in a flow-through respirometer, specimens of *C. jamaicense* reduced $\dot{V}_{O_2}$ by more than 50% for 2 to 3 hr (Fig. 4). Oxygen consumption gradually increased after 5 hr of hypoxia and after 9 hr was near 75% of $\dot{V}_{O_2}$ in normoxia. In normoxia, pleopod activity ranged from 14 to 18 strokes/min. As P_{O_2} decreased to 37 mmHg, pleopod activity at first increased slightly but soon subsided to rates less than those in normoxia.

When introduction of hypoxic water (37 mmHg) followed 12 hr of anoxia, the $\dot{V}_{O_2}$ of *C. jamaicense* was initially just above that observed under normoxia (Fig. 5). The $\dot{V}_{O_2}$ in hypoxia decreased slowly from the rates measured shortly after termination of anoxia. Pleopod activity, which was negligible during anoxia,

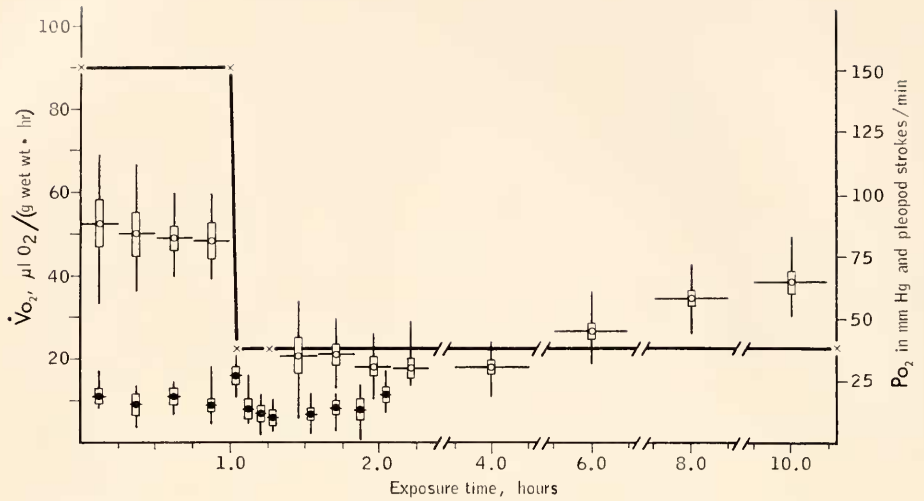

FIGURE 4. Temporal variations in aquatic oxygen consumption (open circles) and pleopod ventilatory rate (solid circles) among specimens of *Callianassa jamaicense* when ambient oxygen tension (crosses on heavy line) is abruptly reduced. Each value is mean rate for five animals. Vertical lines indicate ranges; rectangles indicate standard errors; horizontal lines indicate time spans over which means are taken. Temperature was maintained at $25 \pm 0.2°$ C; salinity was $20 \pm 0.3‰$.

dramatically increased with introduction of hypoxic water. As hypoxic water entered the respiration chamber following 12 hr of anoxia, animals invariably moved to the influent opening of the chamber (Fig. 1) and began rapid ventilation with their pleopods. The accelerated pleopod activity was maintained near 50 strokes/min for *ca.* 30 min after hypoxic water was introduced into the chamber, and animals spent almost all of this time near the influent opening of the respiration chamber. A gradual decrease of pleopod activity paralleled the slowly decreasing $\dot{V}_{O_2}$ which began near the middle of hour 14 and continued through hour 15.

When anoxia was terminated by introducing normoxic (150 mmHg) water, the $\dot{V}_{O_2}$ increased to two times the rates preceding anoxia (Fig. 6). Five hours after anoxia was terminated, $\dot{V}_{O_2}$ approached that observed before anoxia. With the reintroduction of normoxic water, animals moved to the influent opening of the respiration chamber and rapidly ventilated with their pleopods as when hypoxia (37 mmHg) followed anoxia (Fig. 5). However, animals neither remained at the incurrent opening nor maintained accelerated pleopod activity for as long as when hypoxic water followed anoxia.

Field measurements of dissolved oxygen

Burrows of *C. jamaicense* contained very low concentrations of dissolved oxygen when located above the waterline. On Grand Terre Island fluctuating tides exposed numerous burrows along pond margins for periods varying from a few hours to several days. Oxygen tension in water from five active burrows located from 1 to 3 m outside the pond ranged from 0 to 5 mmHg ($\bar{x} = 2.2$ mmHg),

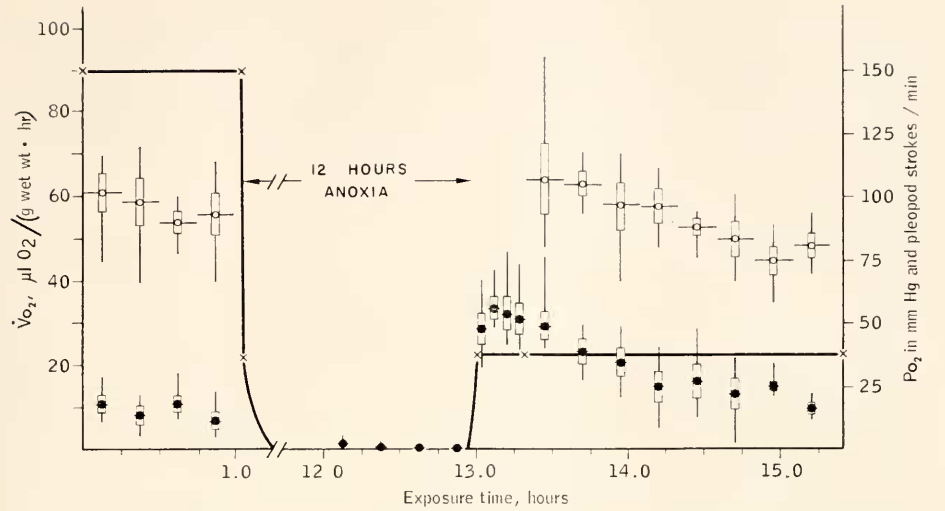

FIGURE 5. Temporal variations in aquatic consumption (open circles) and pleopod ventilatory rates (solid circles) among specimens of *Callianassa jamaicense* when ambient oxygen tension (crosses on heavy line) is dropped to anoxia and then raised to hypoxia. Each value is mean rate for five animals. Vertical lines indicate ranges; rectangles indicate standard errors; horizontal lines indicate time span over which means are taken. Temperature was maintained at 25 ± 0.2° C; salinity was 20 ± 0.3‰.

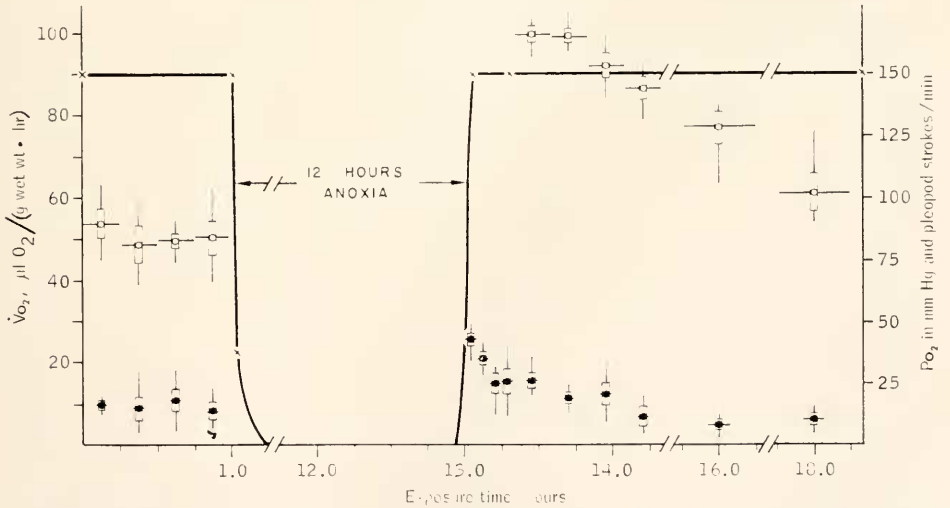

FIGURE 6. Temporal variations in aquatic consumption (open circles) and ventilatory rates (solid circles) among specimens of *Callianassa jamaicense* when ambient oxygen tension (crosses on heavy line) is dropped to anoxia and returned to normoxia. Each value is mean rate for five animals. Vertical lines indicate ranges; rectangles indicate standard errors; horizontal lines indicate time spans over which means are taken. Temperature was maintained at 25 ± 0.2° C; salinity was 20 ± 0.3‰.

which was well below critical oxygen tensions (P_c) established for specimens of *C. jamaicense* in the laboratory. Longer periods of isolation from estuarine pond waters were caused by storm-effected movements of sand which elevated large areas of the pond above water level, sometimes for periods of several months. Excavation of one such area which had been isolated from the pond for 2 months produced numerous living specimens of *C. jamaicense*, although most were moribund; some of these moribund specimens appeared to be occupying portions of burrows above the water table.

Higher and more variable oxygen tensions occurred in burrows at the immediate edge of the pond and just inside the pond. Oxygen tensions in 10 of these burrows, located from 0.2 to 2.0 m inside the pond, ranged from 11 to 119 mmHg ($\bar{x} = 73.4$ mmHg). However, at the time of sampling, oxygen tensions in surface waters were from 151 to 161 mmHg, or well above concentrations in burrows. Oxygen tensions in water of the estuarine pond probably approached these levels only during the periods of photosynthetic activity. Diel cycles of oxygen in water overlying *C. jamaicense* burrows on Grand Terre Island were characterized by decreasing tensions after dark as photosynthesis was replaced by net community oxygen consumption. Diel variations were monitored in October, 1974 (J. Day, personal communication), and P_{O_2} of water overlying *C. jamaicense* burrows remained below the P_c of *C. jamaicense* during a 4 to 5 hr period just before to just after dawn.

Discussion

The limited studies available to von Brand (1946) led him to conclude that decapod crustaceans show little tolerance of anoxia. Extended tolerance of anoxia is, however, one adaptation exhibited by a number of decapods which burrow in potentially hypoxic substrates. For instance, mud-burrowing crayfish survive anoxia four times longer than those inhabiting swift streams (Bovbjerg, 1952). Among the thalassinid decapods, *Upogebia pugettensis* and *Callianassa californiensis* survive anoxia for at least three days (Thompson and Pritchard, 1969) and *Callianassa jamaicense* survives anoxia for three to four days (Fig. 2). These and other thalassinids, such as *Callianassa affinis* in Southern California (Congleton, 1974) and *Callichirus foresti* from west Africa (LeLoeuff and Intes, 1974), are highly specialized for a burrowing existence in shallow, hypoxic, marine substrates, and their tolerance of anoxia is clearly an adaptation to habitat.

Under aquatic anoxia, the longer survival of specimens of *C. jamaicense* when anoxic water is changed daily, compared to survival of specimens when anoxic water is not changed, may reflect the effects of accumulated metabolic wastes. Products of anaerobic metabolism could account for the decrease in pH observed when individuals of *C. jamaicense* are sealed into BOD bottles of anoxic water and left until death occurs. The buffering characteristics of burrow water, particularly in the lower-salinity extremes of *C. jamaicense* habitat, or the ability to exchange anoxic burrow water might thus affect survival of *C. jamaicense* when it is subjected to periods of anoxia in nature. Short-term survival of *C. jamaicense* does not, however, appear to be affected by the physical presence or absence of the burrow, although MacGinitie (1934) reports that a specimen of *Callianassa*

californiensis will soon die if not maintained with its body contacting the wall of a tube. In either anoxia or normoxia, survival of specimens of *C. jamaicense* does not seem to be influenced by whether animals are maintained in plastic tubes or individually in larger bottles and open dishes. The possibility remains, however, that the tube facilitates efficient respiration in hypoxic water.

Survival and oxygen consumption by specimens of *C. jamaicense* in air were investigated despite the lack of direct evidence that this species resorts to aerial respiration in nature. However, on several occasions living animals were collected from substrates which had been exposed for up to 2 months, and on one occasion they were collected from a mud bank more than 1 m above the water table. As negligible concentrations of oxygen are usually found in water of exposed burrows, and as *C. jamaicense* has the ability to survive (Fig. 2) and respire in water-saturated air, occupancy of exposed upper portions of the burrows seems at least a plausible alternative to longterm anoxia. Aerial respiration is best documented among terrestrial and semiterrestrial decapods but is also used on an "emergency" basis by a number of aquatic species (Wolvekamp and Waterman, 1960). For example, *Carcinus maenas* may raise its body and aerially ventilate when stranded in hypoxic ponds (Taylor and Butler, 1973). The humid environment of *Callianassa* burrows fulfills an important requirement for aerial respiration as oxygen diffuses most rapidly across a wet cuticle (Lockwood, 1967).

The lower $\dot{V}_{O_2}$ of *C. jamaicense* in saturated air than in water could be attributed in part to decreased activity under aerial conditions as high P_{O_2} is maintained at the respiratory surface without the need for extensive ventilatory movements. The aerial $\dot{V}_{O_2}$ was less than 40% of aquatic $\dot{V}_{O_2}$ measured in BOD bottles or the flow-through system. This difference in aerial versus aquatic $\dot{V}_{O_2}$ is much greater than that reported for well-adapted semi-terrestrial decapods and suggests that the ability for aerial uptake of oxygen is not particularly well developed. It is not known to what degree *C. jamaicense* depends upon anaerobic pathways under such conditions as at least a partial source of energy. As suggested by Miller *et al.* (1976), it would be interesting to investigate the possible use of anaerobic pathways even at high oxygen tensions.

Within the P_{O_2} range of respiratory independence, $\dot{V}_{O_2}$ of *C. jamaicense* is *ca* 68 μl/(g wet wt·hr) in a stirred BOD bottle from which oxygen is being depleted and 50 to 55 μl/(g wet wt·hr) in a flow-through (10 ml/min) respirometer. Both of these methods involve placement of the animal into a small diameter tube which simulates a burrow and allows the animal to brace itself while ventilating. Measurement of $\dot{V}_{O_2}$ in tubes seems to provide the better index of "routine" (*sensu* Fry, 1975) metabolic rates in burrowing thalassinids as this situation most closely approximates the natural mode of respiration. The reported respiration rates for intermolt specimens of *Callianassa californiensis* over the P_{O_2} range of respiratory independence are for animals not in tubes (Thompson and Pritchard, 1969; Miller *et al.*, 1976; Torres *et al.*, 1977), and these rates vary from *ca.* 18 to *ca.* 34 μl/(g wet wt·hr). Farley and Case (1968) have shown that pleopod activity is clearly greater when a specimen of *Callianassa californiensis* is placed into a small diameter tube than when it is placed into a tube too large for it to brace against tube walls while countering pleopod strokes. In the present study smaller tubes were used in BOD bottles and this necessitated the

use of smaller animals (1.45–3.82 g) than in the flow-through respirometer (4.55–7.13 g); this size difference, as previously suggested by Torres *et al.* (1974), could account for observed differences in $\dot{V}_{O_2}$. Differences in the stirring or flowing of water during measurements of $\dot{V}_{O_2}$ in BOD bottles and the flow-through system may additionally contribute to a difference in $\dot{V}_{O_2}$ measured by those methods, as flow characteristics can engender adaptive respiratory responses (Mangum and van Winkle, 1973).

Regardless of the method of measurement, the metabolic rates here reported for *C. jamaicense* rank among the lower known for crustaceans at similar temperatures (Wolvekamp and Waterman, 1960) and reflect metabolic adaptation to a hypoxic habitat. Low metabolic rates in *Callianassa californiensis* and *Upogebia pugettensis* at 10° C are also considered adaptations to a similarly hypoxic habitat (Thompson and Pritchard, 1969). Montuori (1913) reports a much higher $\dot{V}_{O_2}$ of 132 μl/(g wet wt·hr) in *Callianassa subterranea* and 368 μl/(g wet wt·hr) in *Gebia litoralis* (*Upogebia litoralis*) at 25° C, but experimental conditions of his study differ too greatly to permit detailed comparisons of data.

The low critical oxygen tension (P_c) for *Callianassa jamaicense* likewise suggests a metabolic adaptation. Metabolic regulation is common to a large number of aquatic crustaceans, and van Winkle and Mangum (1975) note that such regulation is expected where the path of oxygen permeation is restricted to an indirect route by way of circulating body fluids. The P_c between 10 and 25 mmHg for *C. jamaicense* (Fig. 3), like that reported for other thalassinids (Thompson and Pritchard, 1969; Miller *et al.*, 1976; Torres *et al.*, 1977) is well below the P_c for most crustaceans (Wolvekamp and Waterman, 1960). Hypothetical curves of oxygen consumption over decreasing P_{O_2}, as predicted by a polynomial model (Mangum and van Winkle, 1973), suggest a P_c for *Upogebia affinis* similar to that reported for *U. pugettensis* but not as low as those in *Callianassa californiensis* or *C. jamaicense*. It has been suggested that the P_c of crustaceans represents the P_{O_2} at which blood pigment fails to become saturated at the gills (Redmond, 1955) or, more recently, that it reflects the initiation of anaerobiosis (Young, 1973). Regardless, maintenance of aerobic respiration until a very low P_{O_2} is reached would seem a conservative adaptation for burrowers in hypoxic substrates.

Present data do not explain the mechanics involved in metabolic regulation by *Callianassa jamaicense* at low P_{O_2}. Neither pleopod activity (Fig. 3) nor heart rate (Thompson and Pritchard, 1969) shows a linear increase with decreasing ambient P_{O_2}. The findings of Torres *et al.* (1977) additionally show that complete immobilization of the pleopods causes no appreciable change in the P_c. However, scaphognathite ventilation rates were not monitored, and it remains to be seen whether scaphognathite ventilation rate, cardiac output, and circulation patterns undergo proportional increases at lowered P_{O_2}. Studies with totally bled specimens of *Callianassa* suggest that at least part of the ability to regulate $\dot{V}_{O_2}$ is due to respiratory properties of the blood itself (Miller *et al.*, 1976).

The increase in pleopod activity at and just below the P_c may reflect an "escape" reaction; escape from low P_{O_2} in nature could be achieved by rapid pleopod ventilation which would replace low P_{O_2} burrow water with higher P_{O_2} water from overhead. Periodic ventilatory pulses, such as those reported for *Callianassa filholi* when specimens are confined to a glass tube (Devine, 1966), may likewise

be such reactions triggered by depletion of oxygen to a concentration near the P_c. Such reactions and taxic responses exhibited during flow-through respirometry suggest the presence of an internal or external oxygen receptor in *C. jamaicense;* Farley and Case (1968) have previously postulated the existence of such a receptor in *Callianassa californiensis* and *C. affinis,* but direct evidence for an oxygen receptor is still lacking for any thalassinid species.

The drop in $\dot{V}_{O_2}$ following abrupt exposure of specimens of *Callianassa jamaicense* to hypoxic water (Fig. 4) indicates that regulation of metabolic rates in low P_{O_2} is dependent upon how fast hypoxia is approached. The decrease in $\dot{V}_{O_2}$ suggests a partial shutdown of aerobic respiration or loss of metabolic regulatory ability unless hypoxia is approached slowly. Mangum (1970) reports aerobic shutdown in bloodworms rapidly introduced into hypoxic water, and Kushins and Mangum (1971) note that metabolic response of the snail, *Nassarius,* depends upon how rapidly hypoxia is approached. Similarly, Hiestand (1931) reports that a crayfish which normally responds as a metabolic regulator will metabolically conform if placed into a small volume of water where P_{O_2} is reduced rapidly or if depletion of oxygen in a large jar commences at less than air saturation. Because $\dot{V}_{O_2}$ of *C. jamaicense* slowly increases after several hours in hypoxic water (Fig. 4), it appears that a time-dependent internal change, such as descrease in pH or re-establishment of diffusion gradients, is linked to ability to regulate $\dot{V}_{O_2}$. This suggests that some degree of low-P_{O_2} acclimation is induced in *C. jamaicense* after six or more hours of hypoxia.

The lowest ambient oxygen tensions in the *Callianassa jamaicense* habitat occur on occasions when burrows are exposed and animals cannot ventilate by pumping water from overhead. An increase in $\dot{V}_{O_2}$ after termination of anoxia (Fig. 6) suggests the development of an oxygen debt under such conditions; a similar compensatory increase occurs in *Callianassa californiensis* and *Upogebia pugettensis* after exposure to anoxia (Thompson and Pritchard, 1969). Although evidence of oxygen debts among crustaceans is meager (Lockwood, 1967), clear evidence of anaerobic glycolysis in *Callianassa californiensis* tends to support this hypothesis (Hawkins, 1971, unpublished M. S. thesis, Oregon State University). Published field observations of several Pacific coast thalassinids (MacGinitie, 1935) and present observations of *Callianassa jamaicense, C. major,* and *C. islagrande* on the Louisiana coast indicate these animals move to the upper portions of the burrows as high tides flood burrows exposed earlier by low tides. Such behavior would facilitate the most rapid exchange of burrow water and payment of an oxygen debt developed during anaerobiosis. The magnitude and duration of elevated $\dot{V}_{O_2}$ rates in *C. jamaicense* following anoxia are determined by the ambient P_{O_2} provided at the termination of anoxia, as evident in comparing Figures 5 and 6. The rate of oxygen uptake under such circumstances is at least passively affected by the blood-to-water gradient of P_{O_2}, and a pattern for metabolic regulation is temporarily supplanted by metabolic conformation and higher respiratory rates in normoxia. It seems very unlikely that the observed differences in post-anoxia $\dot{V}_{O_2}$ rates can be attributed to activity, because activity is greater and maintained at elevated rates for a longer period during slightly elevated $\dot{V}_{O_2}$ in hypoxic water following anoxia (Fig. 5) than during the greatly elevated $\dot{V}_{O_2}$ in normoxic water following anoxia (Fig. 6).

Oxygen uptake via areas of the integument other than gills has not been investigated in *C. jamaicense*, but as these animals have a thin exoskeleton, such extrabranchial uptake of oxygen seems a strong possibility and could prove advantageous in a hypoxic habitat. Although there is no conspicuous morphological evidence of specialized, extrabranchial respiratory surfaces in *C. jamaicense*, accessory pleopodal gill filaments occur on some thalassinids (de Saint Laurent, 1973). The experiments of Torres *et al.* (1977) show no evidence of extrabranchial uptake in pleopods of *Callianassa californiensis*, but further investigations of accessory uptake are warranted; such studies could possibly explain the low oxygen gradients between prebranchial and postbranchial blood reported by Miller *et al.* (1976).

Summary

Callianassa jamaicense survives exposure to aquatic and aerial anoxia for more than 3 days. In normoxic water-saturated air it survives for *ca.* 16 days. The rate of oxygen consumption ($\dot{V}_{O_2}$) in air is less than 40% of $\dot{V}_{O_2}$ in water. Aquatic $\dot{V}_{O_2}$ is regulated above critical oxygen tensions (P_c) of 10 to 25 mmHg when animals are allowed to slowly deplete oxygen from a sealed bottle. Mean aquatic $\dot{V}_{O_2}$ of animals in a flow-through respirometer or in tubes placed into sealed BOD bottles ranges from 50 to 68 μl/(g wet wt·hr) over oxygen tensions (P_{O_2}) above the P_c.

After a 12-hr exposure to anoxic water, $\dot{V}_{O_2}$ is not regulated; post-anoxia $\dot{V}_{O_2}$ in hypoxic water (37 mmHg) is initially less than $\dot{V}_{O_2}$ measured in normoxic water (150 mmHg) before exposure to anoxia; post-anoxia $\dot{V}_{O_2}$ in normoxic water is initially two times the pre-anoxia $\dot{V}_{O_2}$ and suggests the development of an oxygen debt during anoxia. When P_{O_2} of ambient water is abruptly dropped from 150 to 37 mmHg, specimens of *C. jamaicense* exhibit a partial shutdown of aerobic metabolism, but the $\dot{V}_{O_2}$ begins to recover after 6 hr in hypoxia.

When oxygen tension is slowly decreased, pleopod ventilation rate varies little as P_{O_2} changes from 120 to 20 mmHg. The pleopod ventilation rate increases as P_{O_2} falls 20 to 10 mmHg, but decreases below 10 mmHg and stops after several hours under anoxia. The rapid response of taxis and pleopod activity when *C. jamaicense* is exposed to altered P_{O_2} suggests rapid perception of external oxygen levels and provides further circumstantial evidence of an oxygen receptor in thalassinids.

Tolerance of anoxia, metabolic regulation to a low P_c, low metabolic rates, metabolic responses following anoxia, and taxic response to altered P_{O_2} constitute adaptations to the hypoxic habitat of *C. jamaicense*.

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